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# Beta diversity of marine bacteria depends on temporal scale

Stephen M. Hatosy,[1] Jennifer B. H. Martiny,[1] Rohan Sachdeva,[2] Joshua Steele,[2,3] Jed A. Fuhrman,[2] and Adam C. Martiny[1,4,5]

[1]*Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92697 USA*
[2]*Marine Environmental Biology Section, University of Southern California, Los Angeles, California 90089 USA*
[3]*Division of Geological and Planetary Science, California Institute of Technology, Pasadena, California 91125 USA*
[4]*Department of Earth System Science, University of California, Irvine, California 92697 USA*

*Abstract*. Factors controlling the spatial distribution of bacterial diversity have been intensely studied, whereas less is known about temporal changes. To address this, we tested whether the mechanisms that underlie bacterial temporal β-diversity vary across different scales in three marine microbial communities. While seasonal turnover was detected, at least 73% of the community variation occurred at intra-seasonal temporal scales, suggesting that episodic events are important in structuring marine microbial communities. In addition, turnover at different temporal scales appeared to be driven by different factors. Intra-seasonal turnover was significantly correlated to environmental variables such as phosphate and silicate concentrations, while seasonal and interannual turnover were related to nitrate concentration and temporal distance. We observed a strong link between the magnitude of environmental variation and bacterial β-diversity in different communities. Analogous to spatial biogeography, we found different rates of community changes across temporal scales.

*Key words:* *beta diversity; biodiversity; biogeography; distance decay; microbial ecology.*

## Introduction

A well-described pattern in community ecology is the negative relationship between community similarity and physical distance (Harte and Kinzig 1997). Such "distance decay curves" are a directional measure of beta diversity, or variation in community composition among samples (Anderson et al. 2011). This pattern can result from a variety of mechanisms, including environmental heterogeneity, dispersal limitation, migration, and stochastic events (Hubbell 2001, Hanson et al. 2012). The effects of these mechanisms depend on the spatial scale over which they occur, and such scale-dependent patterns have been observed for a variety of taxa in many environments; e.g., plant communities (Nekola and White 1999, Condit et al. 2002), sessile invertebrate and algal communities (Tsujino et al. 2009), and microbial communities (Ramette and Tiedje 2007, Martiny et al. 2011).

Analogous to patterns in space, the abundances of individual taxa as well as the diversity of whole communities are also dynamic over time (Korhonen et al. 2010, Magurran and Henderson 2010). In aquatic environments, studies have shown that microbial communities vary over different timescales (Fuhrman et al. 2006, Kara and Shade 2009, Gilbert et al. 2012, Jones et al. 2012). However, we know little about the relative changes in microbial community composition across different timescales, and the underlying factors that control any such patterns. Because microbial communities commonly consist of thousands of taxa, a beta diversity approach using temporal distance decay curves and variance partitioning across temporal scales can be useful for the investigation of highly complex communities (Anderson et al. 2011). Using these approaches, we analyzed three marine microbial communities to address the following questions: (1) How does beta diversity in marine microbial communities vary over intra-seasonal (<90 days), seasonal, and interannual timescales? (2) Which environmental variables are important drivers of beta diversity at these temporal scales? (3) How do temporal changes in beta diversity compare across three different marine environments? The results of this study indicate that the temporal beta diversity of marine bacterial communities depends on scale and that this diversity is driven in large part by environmental variation.

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[5] Corresponding author. Department of Earth System Science, University of California, Irvine, California 92697 USA. E-mail: amartiny@uci.edu

## Methods

### *San Pedro Basin communities*

We analyzed an eight-year time series of the surface (5 m, SPB5) and a six-year time series of the deep water (890 m, SPB890) from the San Pedro Basin (33.5° N, 118.4° W; Fuhrman et al. 2006) with samples collected once per month. Operational taxonomic units (OTUs) were defined using Automated Ribosomal Intergenic Sequence Analysis (ARISA; Fuhrman et al. 2006). The relative abundance of each OTU was determined by calculating the area under the fluorescence peak relative

to the area under all the peaks. The SPB5 data set consisted of 85 samples and 391 OTUs. The SPB890 data set had 43 samples and 367 OTUs.

### *English Channel community*

The English Channel data set (EC5) was a six-year time series at the L4 Ocean Observatory (50.2° N, 4.2° W; Gilbert et al. 2012). Surface water samples (5 m) were collected once per month between January 2003 and December 2008. OTUs were defined as 97% sequence similarity of the V-6 variable region of 16S rRNA (Gilbert et al. 2012). The data set consisted of 73 samples; a total of 752 028 sequences with an average of 10 301 sequences per sample, and 7614 OTUs identified. We also reduced the number of OTUs to make the EC data set more comparable to the SPB data sets in three ways: (1) We kept the 400 most abundant taxa across all samples, (2) removed taxa that were $<0.1\%$ of the sequences for each sample, and (3) removed taxa that were $<1\%$ of the sequences from each sample. Because yearly autocorrelations (Moran's $I$) and relative intra-seasonal variance (PERMANOVA) of the reduced EC data sets (0.12 to 0.14 and 59% to 60%) were similar to the whole data set (0.15 and 60%), we focused on the whole data set. Proportional abundances from EC5 and SPB were used in the community analysis. The environmental analysis used the variables water temperature and nitrate, phosphate, and silicate concentration because these were variables shared between the three time series. Some of the samples did not have associated environmental data; therefore, the environmental time series are shorter than the community time series.

### *Time series analysis*

Pairwise similarity among all samples was calculated using the Bray-Curtis metric from the "vegan" package in R using untransformed and a square-root transformation of the OTU abundance (Oksanen et al. 2012). The square-root transformation only increased the Moran's $I$ autocorrelation at yearly intervals (0.15–0.20) and the variance decomposition pattern was unchanged (intra-seasonal contribution 62% of the variation and interannual contributing 12% of the variation); therefore, we only included untransformed data for these analyses. The English Channel data were randomly resampled 10 000 times without replacement to standardize the number of sequences in a sample (4101 sequences), and the average of the randomizations was used for further analysis. Temporal distance was calculated as the Euclidean distance between sample dates. Nutrient data (nitrate, phosphate, and silicate) were logarithmically transformed and all environmental data (nutrients and temperature) were normalized to zero with one standard deviation. Environmental similarity was calculated as 1 − Euclidean distance of all environmental variables. We used matrix-based heat maps to color code similarity values and visualize community similarity with the "gplots" package in R (Warnes et al. 2011).

Spectral density analysis was used to investigate the occurrence of seasonal cycles (which we defined as one cycle per year). For this analysis, community similarities were averaged within 30-day windows, and treated as a time series set at monthly intervals. We averaged in these windows because samples were not always collected 30 days apart, so we had a range of day–distance between samples. These averaged time series were demeaned and detrended and the spectral densities were calculated using discrete Fourier transformations via fast Fourier transforms in the "timeSeries" package in R (Wuertz and Chalabi 2012). We used the spatial autocorrelation coefficient, Moran's $I$, to calculate the magnitude of correlation between community and environmental similarities at different temporal distances with the "ape" package in R (Paradis et al. 2004). Individual Bray-Curtis similarities and Euclidean distances were treated as observations, and these observations were grouped into 30-day temporal classes. Environmental samples lacking data for any parameter were removed from the Moran's $I$ calculation. Moran's $I$ coefficients were then calculated between all observations in each temporal class and between temporal classes.

Seasonal (three-month intervals), annual, and intra-seasonal variations were estimated by decomposing the Bray-Curtis community and environmental similarity indices using a permutation analysis of variance (PERMANOVA) with "Adonis" in the "vegan" package in R (Oksanen et al. 2012).

### *Multiple regression on matrices*

We tested whether the turnover slopes were significantly different from zero at four a priori defined temporal scales: $<60$ days (2 months; intra-seasonal turnover), 60–183 days (2–6 months), and 183–365 days (6–12 months; seasonal turnover), and $>365$ days (12 months; interannual turnover). We estimated the significance by randomization of the community similarity matrix at each temporal scale (9999 times).

To examine the factors influencing community similarity, temporal distance, and the similarity of individual environmental variables (silicate, nitrate, phosphate, and water temperature) were regressed on the community similarity matrix using multiple regressions on matrices (MRM; Goslee and Urban 2007, Martiny et al. 2011) at the four temporal scales. This analysis estimated regression coefficients and tested for significance by permuting the community similarity matrix and holding the environmental and temporal distance matrices constant. The predictor variables were standardized to a mean of zero and standard deviation of one, and the significance of the partial correlation coefficients were tested using a one-tailed $t$ test.

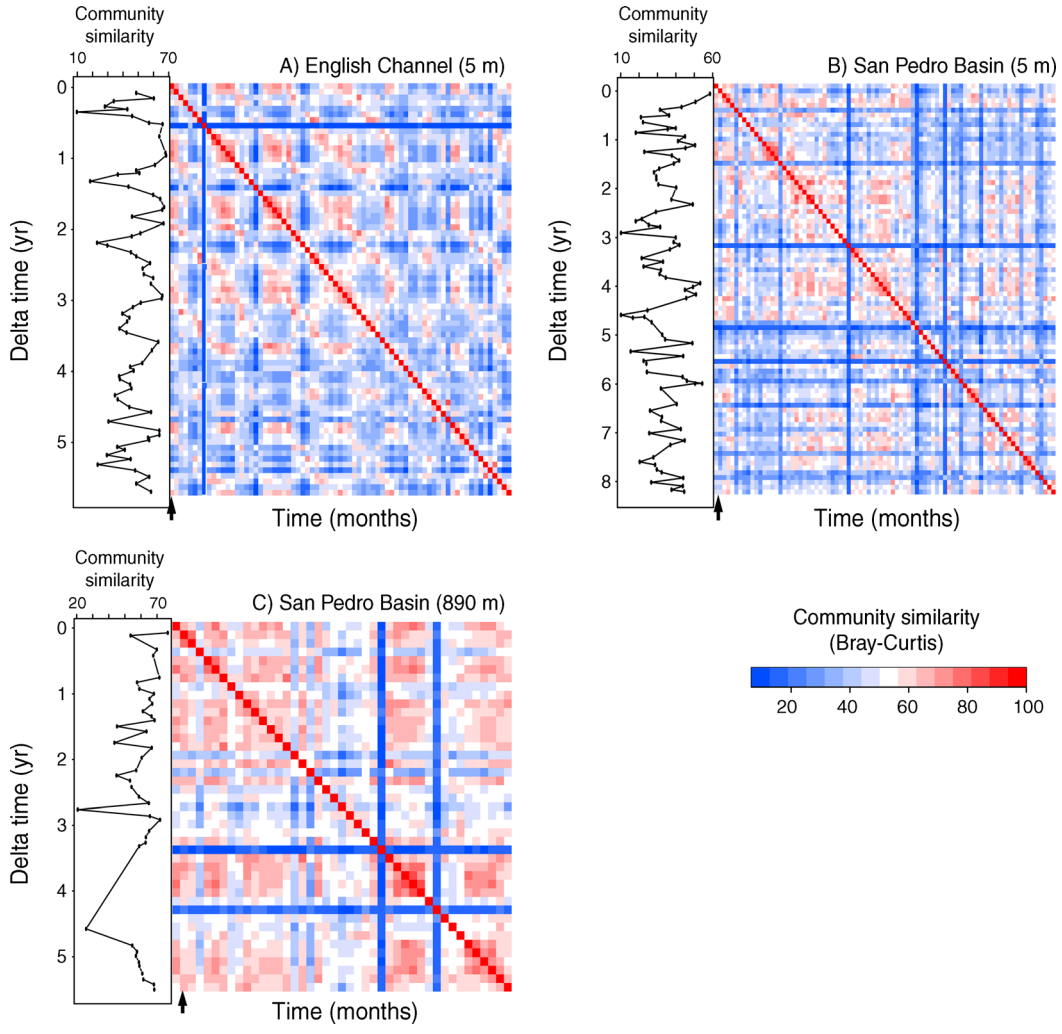


FIG. 1. Heat maps of pairwise community similarity over time for (A) the English Channel (at 5 m depth), (B) San Pedro Basin (at 5 m depth), and (C) San Pedro Basin (at 890 m depth). Community similarity is measured as the Bray-Curtis percentage similarity. Delta time is the distance between two samples in years. Hot colors represent high similarity between two samples. Cool colors represent low similarity between two samples. The red diagonals represent the similarity of each sample compared to itself. The panels to the left of the heat maps are cross-sections of one sample compared to all other samples. Arrows show the samples used in cross-sections. Plots represent different time durations but were resized.

## RESULTS

To characterize and quantify the temporal turnover of marine microbial composition, we first calculated community pairwise similarity between all samples at a location. This was done for communities from the English Channel surface waters (EC5), San Pedro Basin surface waters (SPB5) and deep water (SPB890; Fig. 1A–C). Over the entire time series, community similarity varied widely in all three communities (Appendix A: Table A1). The surface communities at EC5 and SPB5 had nearly identical global average similarities superimposed with periods of high and low similarity at 12-month intervals (Appendix A: Table A1). Specifically, the 30-day averages of similarity at EC5 and SPB5 oscillated between 0.28 and 0.57 at one-year periods. Seasonal turnover in surface communities could also be seen from the cross-section of sample 1 compared to all other samples (Fig. 1A, B). In comparison, the deep-water community at SPB890 varied irregularly between similarity values of 0.44 and 0.72 (Fig. 1C).

Plots of community similarity vs. temporal distance showed periodic patterns for the surface regions (Fig. 2A, B), so we next estimated the frequencies of oscillation with a spectral density analysis and Moran's $I$ correlation analysis. The spectral density analysis showed a strong peak at one cycle per year for the surface communities at the EC5 and SPB5 sites (Appendix B: Fig. B1), confirming the visual observations of seasonal changes in both regions. In contrast, the SPB890 community did not show any periodic signal. The Moran's $I$ analysis also supported the spectral analysis because it showed that the surface

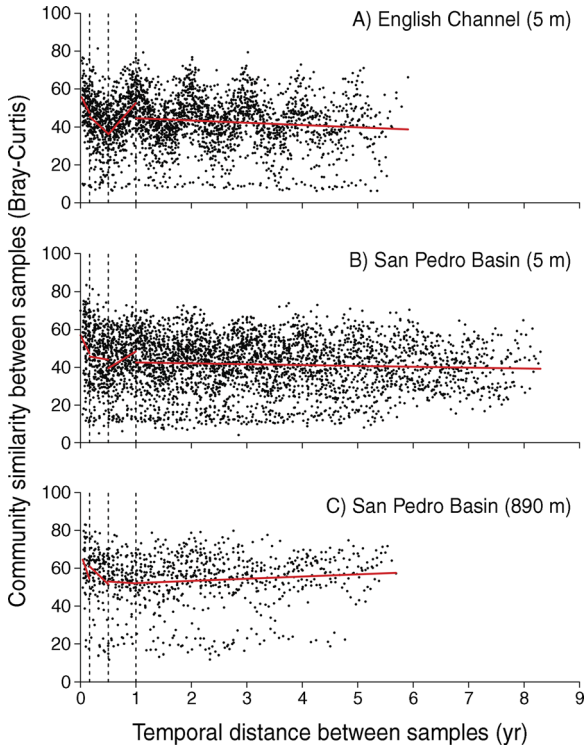


FIG. 2. Temporal decay curves for bacterial communities at the English Channel (at a depth of 5 m), San Pedro Basin (at a depth of 5 m), and San Pedro Basin (at a depth of 890 m). Community similarity is measured as the Bray-Curtis percentage similarity, and delta time is the time distance between two samples in years. Red lines represent linear regressions at different temporal scales (0–60 days, 61–183 days, 184–365 days, and >365 days).

communities were seasonally autocorrelated at one-year intervals (Appendix B: Fig. B2). In addition, Moran's *I* revealed that seasonal variation of the microbial community was 3.9 times greater at EC5 compared to SPB5 (Appendix B: Fig. B2A, B).

We next asked whether the rate of community turnover (i.e., the slope of the temporal distance decay curve) varied over different temporal scales. We observed a significant (MRM; $P < 0.0001$) interannual decline in the mean similarity in the EC surface communities, whereas we did not observe this trend at the two SPB sites (Fig. 2, Table 1). On average, overall community similarity declined 1.2% per year at the EC5 from an initial average similarity of 0.44 to 0.40. We also found extensive community variation at intra-seasonal time intervals (Figs. 1 and 2). For instance, samples that were collected 28 days apart ranged between 0.098 and 0.71 similarity. At no point were two samples completely different or identical (Fig. 2). As an example of the importance of episodic events on marine community composition, we observed the occurrences of nearly unique communities at all three regions (illustrated by the solid blue columns and rows in Fig. 1). Such events occurred as few as one time at EC5 and as many as seven times at SPB5. Furthermore, the decay of community similarity at all three sites during the first 60 days was significantly higher compared to the period between 60 and 183 days (Table 1, Fig. 2). In other words, the community changed more rapidly over short timescales than seasonally or interannually.

Based on the MRM analyses, it was clear that community turnover varied at different temporal scales. To examine this further, we next decomposed the similarity variation into annual, seasonal, and intra-seasonal (<90 days) components to quantify the

TABLE 1. Community turnover regression and multiple regression on matrices (MRM) at different temporal scales at EC5 (English Channel, 5 m depth), SPB5 (San Pedro Basin, 5 m depth), and SPB890 (San Pedro Basin, 890 m depth).

| Site and temporal scale (d) | Community turnover | Temporal distance | Silicate | Nitrate + nitrite | Phosphate | Water temperature |
|---|---|---|---|---|---|---|
| EC5 | | | | | | |
| <60 | −56.8 (0.017) | n.s. | 0.27 (0.027) | n.s. | 0.36 (0.019) | n.s. |
| 60–183 | −27.1 (<0.001) | 2.02 (0.001) | n.s. | 0.41 (0.001) | 0.15 (0.038) | n.s. |
| 183–365 | 33.4 (<0.001) | −2.24 (0.001) | n.s. | 0.33 (0.002) | n.s. | n.s. |
| >365 | −1.20 (0.024) | n.s | n.s | 0.51 (0.001) | n.s. | n.s. |
| SPB5 | | | | | | |
| <60 | −58.8 (0.012) | n.d. | n.d. | n.d. | n.d. | n.d. |
| 60–183 | −7.9 (0.286) | 1.52 (0.022) | n.s. | n.s. | n.s. | n.s. |
| 183–365 | 17.6 (0.001) | −1.29 (0.081) | n.s. | n.s. | n.s. | n.s. |
| >365 | −0.45 (0.14) | n.s. | n.s. | n.s. | n.s. | 0.19 (0.036) |
| SPB890 | | | | | | |
| <60 | −86.0 (0.014) | n.d. | n.d. | n.d. | n.d. | n.d. |
| 60–183 | −28.0 (0.002) | n.d. | n.d. | n.d. | n.d. | n.d. |
| 183–365 | 0.099 (0.496) | n.d. | n.d. | n.d. | n.d. | n.d. |
| >365 | 1.15 (0.108) | n.d. | n.d. | n.d. | n.d. | n.d. |

*Notes:* Community turnover is the regression slope reported as percentage points per year (*P* value in parentheses). MRM slopes are reported as regression slope (*P* value in parentheses). Nutrient concentrations were $\log_{10}$-transformed before analysis. Abbreviations are: n.s., not significant; n.d., not determined (not enough environmental data from SPB890 to calculate an MRM analysis, and for SPB5, there were only enough data for <185 days).

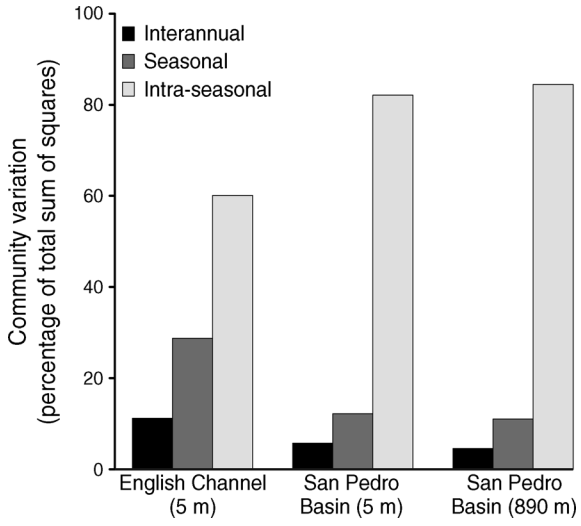


FIG. 3. Variance decomposition of community similarity into annual, seasonal, and intra-seasonal components for the English Channel (5 m depth), the San Pedro Basin (5 m depth), and the San Pedro Basin (890 m depth). The variance decomposition was done using PERMANOVA on a Bray-Curtis similarity matrix for all samples from each region.

contribution of different timescales to overall community variation. The majority of variation (>60%) in all regions was associated with short-term changes, whereas the seasonal component contributed between 11% and 23% (Fig. 3). Interannual variation was the least variable and represented <11% of the total variation.

What factors controlled these temporal patterns? We found that different environmental variables as well as temporal distance explained the turnover at different temporal scales. At the 30–60 day temporal scale, the rapid turnover at EC5 was correlated with changes in phosphate and silicate concentration, while turnover was correlated to temporal distance alone at SPB5 (Table 1). Within the 60–183 day and 183–365 day temporal scales, turnover at EC5 appeared to be correlated to nitrate + nitrite and phosphate concentration and temporal distance; however, at SPB5 turnover was again correlated with temporal distance (Table 1). Over 365 days, community turnover at EC5 could be explained by nitrate + nitrite concentration, while at SPB5 turnover was correlated to water temperature (Table 1). Thus, it was clear that different factors and beta diversity were correlated at different temporal scales.

Given that environmental factors appeared to be driving much of the temporal beta diversity, we also directly investigated the temporal patterns of environmental conditions. First, we observed a yearly repeating seasonal oscillation in environmental similarity at the two surface sites (Appendix B: Fig. B3). This seasonality was found in temperature and nitrate, phosphate, and silicate concentrations at EC5 (Appendix B: Fig. B4A), whereas only temperature and phosphate were seasonally changing at the SPB5 site. However, the absolute seasonal change in temperature was slightly higher at EC5 (~7–8°C) than SPB5 (~5–6°C) (Appendix B: Fig. B4). In contrast, environmental conditions at the SPB890 deep-water site showed little seasonality (Appendix B: Fig. B3C). Overall, there were stronger seasonal changes at EC5 compared to SPB5 compared to SPB890, whereas interannual changes were limited across all three regions. However, all three sites also displayed extensive variation (>47%) at the intra-seasonal scale (Appendix B: Fig. B5).

## DISCUSSION

Analogous to many studies of spatial biogeography (Preston 1960, Nekola and White 1999, Ramette and Tiedje 2007, Martiny et al. 2011), we saw distinct patterns of bacterial turnover over time at three different temporal scales (i.e., seasonal, interannual, and intra-seasonal) in several ocean regions. Thus, temporal beta diversity of bacteria appears to depend on scale, just as for spatial beta diversity.

Specifically, within seasons (~0–60 days), we observed the highest community turnover. High short-term community turnover has also been described in other freshwater and marine microbial studies (Kara and Shade 2009, Korhonen et al. 2010), suggesting this pattern is a general phenomenon. Such rapid changes can be driven by at least two mechanisms. First, microbial composition may be tracking the environment. In support of this mechanism, we observed that most variation in environmental conditions occurs at intra-seasonal scales at all three sites (Fig. 3). Further, the rapid compositional turnover at EC5 was correlated with changes in phosphate and silicate concentration (Table 1). Such a correlation might suggest that bacterial communities are tracking these nutrients, although it is also possible that they co-vary with phytoplankton communities, which are responding to changes in nutrient concentration at these scales (Kent et al. 2007). High variation in environmental conditions over short time intervals (<1 month) has also been observed in other coastal marine systems (Cloern and Nichols 1985), whereas open ocean regions are generally less variable. Thus, if environmental variation is the key driver of short-term microbial beta diversity, we would expect that intra-seasonal beta diversity will generally be lower in open ocean regions than in coastal marine communities.

A second mechanism that could contribute to the rapid turnover of marine bacteria within seasons is ecological drift (Hubbell 2001). Whereas samples taken a few days apart from one another may share a "historical" connection (their composition may be highly similar because there has not been time for taxon abundance to respond to new environmental conditions), this connection should be less apparent after several weeks, as mixing of water parcels takes place. In this way, ecological drift could contribute to the

"steepness" of the distance decay curve on short timescales, just as it appears to do at small spatial scales (Condit et al. 2002, Martiny et al. 2011). In support of this mechanism, we observed a significant relationship between temporal distance and microbial composition at short timescales (<60 days) in the SPB5 data set even after controlling for the measured environmental variables. However, this pattern can be due to unmeasured abiotic and biotic variables (Hanson et al. 2012); thus, additional work is needed to assess the importance of ecological drift for temporal beta diversity in microbial communities. It is possible that differences between communities could be attributed to analytical artifacts since DNA fingerprinting and sequencing may introduce various errors as well as likely only identify a subset of the microbial biomass (Sogin et al. 2006). However, such analytical variation may contribute little to the temporal patterns. Jones and colleagues (2012) found that Automated Ribosomal Intergenic Sequence Analysis (ARISA) could differentiate communities that were >5% different based on the Sorensen index. So it appears unlikely that analytical artifacts would influence the different temporal patterns of community changes observed.

Within the 60–183 day and 183–365 day temporal scales, the average absolute rate of community change declined in comparison to the first 60 days. In the near-surface communities, we also saw a seasonal oscillation that has been observed in previous studies (Fuhrman et al. 2006, Gilbert et al. 2012). The deep-water community also varied between seasons, but not in a repeatable pattern. Thus, the bacterial community composition at depth may not be responding immediately to changes in primary production, an interaction that has been described across lakes (Kent et al. 2007). It is also likely that communities at this depth are driven by non-repeatable fluxes in particulate organic matter. The seasonal variation at the English Channel is nearly three times greater than at the surface of the San Pedro Basin, which is likely due to a stronger absolute seasonal change in environmental variation at EC5 (Appendix B: Fig. B3A, B). The relationship between the strength of community and environmental turnover has also been observed in the seasonal dynamics of amphibians across latitudes (Canavero et al. 2009), and thus is not limited to marine microorganisms.

At the interannual timescale, temporal community turnover was correlated with temporal distance and environmental similarity. As discussed, one interpretation of the turnover at EC5 is that this pattern may be caused by historical differences due to ecological or genetic drift because of the correlation with temporal distance after controlling for environmental effects. Alternatively, surface communities are responding to environmental variation at longer timescales. The latter interpretation is supported by our analyses as beta diversity at this timescale is significantly correlated with nitrate + nitrite at EC5 and with water temperature at SPB5 (Table 1). Thus, variation of surface communities at this temporal scale is possibly driven by long-term changes in environmental conditions, including the North Atlantic Oscillation and El Niño/Southern Oscillation events. In contrast, we did not observe any systematic interannual trend in community composition or environmental similarity at 890 m, a pattern that is similar to the general pattern of interannual stability seen in freshwater systems (Shade et al. 2007, Crump et al. 2009).

It should be noted that in our comparison of these ocean regions, different methods are used to infer taxonomy (ARISA fingerprinting vs. 16S rRNA sequencing). The English Channel site has almost 20 times more identified taxa than either region of the San Pedro Basin (Appendix A: Table A1). Thus, it is possible that a methodological difference influences observed turnover patterns between the communities (Anderson et al. 2011). However, there are four reasons why the differences may be biological and not methodological. First, The EC community composition diversity was reduced to simulate the community resolution limits of ARISA, but this did not affect the patterns. Second, ARISA is used for both regions of the San Pedro Basin, yet the deep-water community did not have recurrent seasonal variations. Third, both surface communities share many similarities in the overall temporal scale patterns. Last, the magnitude of environmental variation follows the same pattern as community variation across the regions and temporal scales. Thus, the patterns observed do not appear to be an artifact of methodologies.

Decay patterns of community composition occur across space and time, and across taxonomic groups (Nekola and White 1999, Korhonen et al. 2010). For macroorganisms, the pattern at each scale can sometimes be attributed to a particular process. For large organisms, this includes sampling error at small scales, ecological processes at intermediate scales, and evolutionary processes at large scales (e.g., Preston 1960, Soininen 2010). For marine bacteria, it is possible that similar processes control community composition and turnover at different temporal scales. Here, ecological processes, namely responses to fluctuations in the environmental conditions, appear to influence beta diversity at the intra-seasonal, seasonal, and interannual scales. However, different environmental factors control changes in microbial communities at different temporal scales. In addition to direct environmental selection, we also see some evidence of ecological drift, whereby past environmental conditions can influence beta diversity at short timescales. Our analysis demonstrates that microbial communities show unique patterns of temporal beta diversity depending on the timescale and environmental conditions. Thus, predicting how microbial communities will respond to future environmental changes requires knowledge of the factors influencing communities at multiple temporal scales.

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Supplemental Material

**Appendix A**

Supplemental information of the sample locations including sample depth, latitude and longitude, sampling duration, number of samples, number of operational taxonomic units, and community similarity values (*Ecological Archives* E094-172-A1).

**Appendix B**

Supplemental results: power spectra, Moran's *I* correlograms, and variance decomposition (*Ecological Archives* E094-172-A2).